

ORIGIN OF THE ANGIOSPERMS: NEED FOR A BROADENED OUTLOOK ¹

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WE ARE HEARING more and more of late, in various fields of human endeavor, regarding the significance of a "New Look." Much is being spoken and written regarding the necessity for a "New Systematics" and for a "New Morphology." All of us will, I believe, readily admit the need for new methodologies and for new points of view in the development of botanical science. However, if real progress is to be made, it is essential to analyze trends of putative originality to determine whether they are soundly conceived and of productive potentialities. This is particularly true in dealing with such complex and difficult problems as to how, when, and where the angiosperms originated, how they became so highly diversified and so widely distributed, and how they should be classified in a system of truly natural relationships.

The "New Morphology" commonly involves the basic assumption — to quote a recent exponent ² — that a comparison of the organs of angiosperms and of lower plants only makes sense if the former are abandoned as a starting point and if we allow ourselves to be guided only by paleobotanical evidence in the direction of evolutionary development. Is the sweeping generalization that we should be guided in the study of angiospermic phylogeny and classification solely by paleobotanical evidence a sound one? When shorn of its psilophytalian halo, the "New Morphology" frequently consists in practice of highly speculative attempts to homologize specific parts — even teratological ones — of a few selected angiosperms with those of ancient land plants. In so doing, scant attention is given to long stretches of geological time during which profound morphological changes are likely to have occurred. Furthermore, the fact that many salient trends of morphological specialization are adequately preserved in the huge assemblage of surviving angiosperms is overlooked or ignored. This procedure of the "New Morphology" is not new, since it is essentially similar to that utilized in the past, for example, in interpreting the Magnoliaceae in terms of the Bennettitales and the Amentiferae in homology with the Gnetales.

It is not my intention to belittle the great contributions that the study of the Psilophytales and of other ancient land plants have made to a clearer understanding of the stem and of its appendages, but rather to

¹ Invitation paper read before the Paleobotanical Section of the Botanical Society of America, Sept. 13, 1948.

² LAM, H. J. Classification and the New Morphology. *Acta Biotheoretica* 8: 109. 1948.

emphasize the necessity for much broadened outlooks in discussion of the origin and the relationships of the angiosperms. We need "new looks," but they should be comprehensive, rather than narrow and excessively speculative ones. There are as grave dangers in indiscriminately interpreting selected structures of living angiosperms solely in terms of ancient Land Plants as there formerly were in studying fossil plants with excessive dependence upon the classical concept of the stem and leaf.

For example, recent attempts to establish the Sarcopodaceae as a new family of gymnosperms, and to utilize it as support of a stachyosporous line of angiosperms provide cogent evidence of inherent dangers in the methodologies of the "New Morphology." The authors³ of the new family have been forced to admit that *Sarcopus aberrans* is a species of the santalaceous genus *Exocarpus* and to change the name of the family to Exocarpaceae. If the Exocarpaceae are to be removed from the Santalaceae and placed in closer relationship to the gymnosperms such a transfer should be based, not solely upon superficial examinations of the flower of a single species, but upon comprehensive cytological, embryological, anatomical and general morphological studies of *Exocarpus* in comparison with other genera of the Santalaceae and of other families of the Olacales. In addition, phylogenetic conclusions should be in harmony with salient trends of morphological specialization in the angiosperms as a whole. In the case of *Exocarpus*, even an examination of the pollen and the xylem afford pertinent evidence in refutation of such premature phylogenetic generalizations. Similar objections apply in the use of selected parts of such genera as *Casuarina*, *Salix*, *Ricinus*, *Portulaca*, *Calothamnus*, etc. when divorced from their context in the dicotyledons as a whole.

It should be emphasized in these connections that diversified investigations of surviving angiosperms provide the only available means at present of morphologically characterizing this great group of the vascular plants, and for recognizing and of accurately identifying ancestral forms when found. Each botanical discipline, Taxonomy, Paleobotany, Phyto-geography, Cytology, Embryology, Anatomy, Developmental Morphology, Genetics, etc., has important contributions to make in the ultimate solution of various aspects of the great central mysteries, but the limitations of each field of research in the solution of specific problems of phylogeny and relationship should be clearly visualized and freely admitted.

The Land Plants from the Psilophytales onward are aptly designated by some the Tracheophyta, since they are characterized throughout by the formation of tracheary tissue. The constituent cells of this tissue obviously perform two fundamentally important functions, 1) the conduction of water and solutes from the absorbing to the transpiring parts of the plant, and 2) the provision of mechanical strength in parts where they occur. The former function is facilitated by peculiarities in the

³ GAGNEPAIN, F. & ED. BOUREAU. Une nouvelle famille de Gymnospermes: les Sarcopodacées. Bull. Soc. Bot. France. 93: 313-320. 1946.

——— & ———. Nouvelles considérations systématiques à propos du *Sarcopus aberrans* Gagnepain. Bull. Soc. Bot. France. 94: 182-185. 1947.

form of the cells and by the loss of their cytoplasmic contents at maturity, the latter function by the remarkable physical structure and the chemical composition of their cell walls. The major trends of phylogenetic modification of the tracheary tissue of the Land Plants are associated with changes of equilibrium between these two fundamentally important physiological functions. In the case of most dicotyledons, there is a striking division of labor within the vascular tissues, certain linear series of tracheids becoming modified to form vessel members, whereas others assume an increasingly fiberlike form and may at times take on a storage function in addition to an exaggerated mechanical one. These salient trends of evolutionary specialization of the tracheary tissues are largely unidirectional and irreversible, and are fully and adequately preserved in surviving angiosperms. There fortunately are no serious missing links in these phylogenetic chains and it is not essential, for example, to search geological strata for vesselless pro-angiosperms since ancestral types of primitive xylem occur in living representatives of both the dicotyledons and the monocotyledons.

Before discussing the significance and the limitations of these phylogenies in the study of plant relationships, it is essential to comment briefly upon the character of the evidence upon which they are based. Large collections of materials of woody dicotyledons have gradually been accumulated at Yale, Oxford, Harvard and many other institutions. These collections when supplemented by herbarium specimens have afforded material for the study of many genera of *all* of the principal families of the angiosperms. In addition, sufficient developmental investigations have been made so that it now is possible to visualize salient trends of specialization of the xylem in terms of a phylogeny of successively modified ontogenies. In other words, the evolutionary picture has emerged, and has become increasingly distinct, as larger and larger volumes of data have been analyzed from the angiosperms and the gymnosperms as a whole. It has crystallized solely from the study of the vascular tissues themselves, and entirely independently of assumptions regarding the putative primitiveness of specific representatives of the dicotyledons or monocotyledons. Furthermore, these particular trends of evolutionary specialization cannot be read in a reverse direction, since no one is likely to argue, in the light of our present knowledge of the Tracheophyta, that tracheids originated from the dissociated members of vessels.

What then are some of the more important contributions that a knowledge of these unusually extensive and reliable vascular phylogenies can make in discussions of the origin and the relationships of the angiosperms? Obviously it would be possible to arrange the angiosperms according to a system of increasing specialization of the vascular tissues, but such a system of classification would prove to be as unsatisfactory as others that have been based primarily upon the study of restricted parts of plants. If a truly natural classification is to be attained, it must be based upon the analysis and the harmonization of evidence from *all* organs, tissues and parts. This is due to the fact that the morphological specializations of

different structures commonly are not synchronized. The flower or one of its parts may be changing rapidly at the time when the vascular tissues exhibit morphological stability or *vice versa*. In studying plant relationships, evidence from the vascular tissues is in general more significant in negations than in affirmative conclusions. This is due to the frequent occurrence of parallel trends of evolution in the various organs and tissues of the Land Plants. Thus, although it is impossible to derive truly primitive forms of xylem from highly specialized ones, close structural similarities may be due to parallel or convergent development rather than necessarily to close genetic relationship.

In illustration of these basic considerations, let us turn to a specific discussion of the present revival of assumptions regarding the possibility of deriving the angiosperms from the Coniferales, Gnetales, Bennettitales or Williamsoniales.

The Lycopsidea, Sphenopsida, and most of the Pteropsida are characterized by having essentially similar ontogenetic sequences in the development of their tracheary tissue. In a fully elongated axis, as seen in radial longitudinal sections, the earlier formed tracheary cells have loosely coiled helical thickenings, although they may be preceded at times by tracheids with annular thickenings. These cells are succeeded by tracheary cells having compactly coiled helical thickenings of very low pitch, and these in turn by elements exhibiting transitions between scalariformly reticulate and scalariformly bordered pitted walls. In certain groups of Land Plants, e.g., many Lycopsidea, Sphenopsida, and ferns, the subsequently formed tracheids have dominantly scalariform pitting, whereas in other groups, e.g., many seed ferns, Cordaitales and Cycadales, there are subsequent transitions between scalariform bordered pits and approximately circular ones of varying number and distributional patterns.

In the Ginkgoales, Coniferales, and Gnetales, this *normal* ontogenetic sequence, characteristic of a vast majority of the Land Plants, is profoundly modified. True scalariform bordered pitting is eliminated and circular bordered pits are formed in the earlier stages of the ontogenetic sequence, even in the first-formed tracheary cells with loosely coiled helical thickenings. This modification of the primary vascular tissues is firmly established in the Coniferales and Gnetales and is indicative of an ancient trend of drastic anatomical specialization. In the latter order, vessels developed from tracheids having circular bordered pits. On the contrary, in the stems of angiosperms, which have retained a primitive type of vesselless xylem, the ontogenetic sequence is of the normal type, and vessels have developed in both dicotyledons and monocotyledons, as in *Pteridium*, by the modification of tracheids with scalariform bordered pitting. Such fundamentally significant anatomical differences form an insuperable barrier to a derivation of the angiosperms from the Coniferales or the Gnetales. Thus, the presence of vessels in both the Gnetales and the angiosperms, which has so frequently been cited as evidence of relationship, actually negates such relationship. There are similarities between the end products of tracheary specialization in *Gnetum* and certain of the dicotyledons,

but they have arisen by entirely different developmental changes.

What then are the possibilities of deriving the angiosperms from the Bennettitales or Williamsoniales? Here the evidence from the vascular tissues alone is inconclusive. Although similar transitions between tracheids with scalariform and circular bordered pitting occur in the secondary xylem of vesselless dicotyledons and of certain cycadeoideas, the similarity is not indicative necessarily of close relationship, since it may be due to parallel evolutionary development. Furthermore, the possibility of deriving the angiosperms from the Bennettitales or Williamsoniales, as also from the Corystospermaceae or Caytoniales, appears to be negated by evidence from other parts of the plants, particularly the reproductive ones.

It is essential at this point to digress briefly for comment upon a recent attempt to derive certain ranalian families from the Bennettitales, and to arrange them in a linear evolutionary series.⁴ This effort is based largely upon the reported discovery of a new type of tracheary element in the Magnoliceae and supposedly related families, and affords a pertinent illustration of inherent dangers in a narrow anatomical look. The cells in question are of a well known tracheary type which was fully discussed at meetings of the Committee on Nomenclature of the International Association of Wood Anatomists. They are new only through changes in terminology.⁵ A broad anatomical look at the vascular plants as a whole reveals the fact that tracheids with a similar configuration of bordered pitting occur, not only in the Bennettitales but also in other gymnosperms, and in many orders of the dicotyledons as well as in certain families of the Ranales. Furthermore, the true significance of the configurations cannot be fully understood without reference to accumulated data regarding the physical structure of the walls of tracheary cells. It should be emphasized in passing that it is such sweeping generalizations, based upon limited and inadequate data, that have raised uncertainties and doubts in the minds of many botanists regarding the value and the reliability of anatomical evidence in the study of phylogeny.

Up to this point, I may have given the impression of an excessively pessimistic look at the problem of the origin of the angiosperms, in which the only certainties are negations and in which potential ancestors of the angiosperms are successively eliminated. However, if real progress is to be made in the solution of the great mystery, it is essential periodically to differentiate the *wheat* of reliable cumulative evidence from the *chaff* of excessive speculation. As a matter of fact, I am quite optimistic regarding advances that can be made in the near future, provided investigators in various botanical disciplines cooperate more actively in providing essential data for a well coordinated attack along a broad morphological front.

⁴ LEMESLE, ROBERT. Les divers types de fibres à ponctuations aréolées chez les dicotylédones apocarpiques les plus archaïques et leur rôle dans la phylogénie. *Ann. Sci. Nat. Bot. et Biol. Végétale* 7: 19–40. 1946.

⁵ BAILEY, I. W. The problem of differentiating and classifying tracheids, fiber-tracheids, and libriform wood fibers. *Tropical Woods* 45: 18–23. 1936.

Our knowledge of the vascular tissues of Land Plants has advanced to a position where it can aid materially in planning such a campaign, in avoiding serious pitfalls, and in restraining fruitless sorties in haphazard directions. Thus, the tracheary phylogenies, that are so clearly and fully preserved in surviving angiosperms, provide us with significant clues regarding the general habit of growth of ancestral dicotyledons. This is due to the fact that, in the various dicotyledonous families, herbs, vines, lianas, succulents, aquatics and extreme xerophytes exhibit a high degree of specialization of the vascular tissues, whereas vesselless xylem and the less modified forms of vessel-bearing xylem occur in large woody perennials, viz. shrubs or trees. Such facts negate the possibility not only of deriving structurally primitive types of arboreal dicotyledons from herbaceous ancestors, but also of deriving the monocotyledons from herbaceous dicotyledons, e.g., the Ranunculaceae. If the angiosperms are monophyletic, the monocotyledons and the dicotyledons must have diverged at an early date, since vessels have developed independently in the two groups.

Of the nearly 100 species of living dicotyledons, which have a primitive vesselless type of both primary and secondary xylem, all occur within the order Ranales, as broadly conceived by Engler and Prantl. Furthermore, an unusually complete record of the origin of vessels and of salient trends of specialization of the xylem is preserved within this order. That these occurrences are not purely fortuitous, and may have significant implications, is suggested by accumulating data regarding the pollen morphology of seed-bearing plants. Most of the families and orders of the dicotyledons are characterized by having tricolpate pollen or types of pollen that appear to have been derived phylogenetically from such grains. Tricolpate pollen is not known to occur in any other group of seed-bearing plants and therefore is indicative of a highly distinctive trend of specialization in pollen morphology. Monocolpate pollen, which is characteristic of so many seed ferns, Bennettitales, Cycadales and Ginkgoales, is of common occurrence in monocotyledons, but is largely confined in the dicotyledons to a number of the more woody families of the Ranales. In other words, insofar as I have been able to determine, the Ranales are the only order of the angiosperms in which both monocolpate and tricolpate pollen occur.

However, it was the remarkable carpels and stamens of a previously undescribed family of the Ranales, viz. the Degeneriaceae, which induced Dr. A. C. Smith and myself to initiate a series of comprehensive coordinated investigations of ranalian families, in which others are now actively cooperating. I have already reported, earlier in these meetings, upon the primitive, unsealed, conduplicate ranalian carpel and concerning its salient trends of specialization in different ranalian families. There are equally significant transitions in the Ranales between broad microsporophylls and stamens of a more conventional form. These investigations at least justify a "New Look" at the flower of the angiosperms as a whole. Comprehensive studies of the various orders and families of living angiosperms should eventually provide adequate accumulations of evidence

for determining whether the putative lines of stachyosporous dicotyledons actually are such or have been derived from a phyllosporous one such as characterizes the Ranales. It should be noted in this connection that detailed and extensive investigations of other parts of living angiosperms, viz. the leaf, fruit, seed, embryo-sac, seedling, etc. are essential in synthesizing a picture of a primitive angiosperm or angiosperms to serve as a guide to paleobotanists in their search for pro-angiosperms.

Allow me to conclude my remarks with a few brief comments upon those parts of the Earth's surface which appear to me to offer the most promising fields for future explorations. It is the living floras of northern Australia, New Guinea, New Caledonia, and Fiji and adjacent regions northward to southern China that have yielded and are continuing to yield the richest crop of missing links in the chains of angiospermic phylogenies. For example, of the nine known genera of primitive vesselless dicotyledons, five occur on New Caledonia and three are endemic on that island. Only a beginning has been made in the exploration of many of these floras and a continuous flow of significant new plants may be anticipated for some time to come as more and more complete collections are assembled. Furthermore, these living floras of southern latitudes have already yielded more structurally primitive dicotyledons than have all of the known fossil floras of northern latitudes. Therefore, I am inclined to question the assumption of a northern origin for the angiosperms at least until the Tertiary and Mesozoic rocks of these southern lands have been adequately explored. It should be emphasized, in addition, that comparatively little is known regarding the seed-ferns of the *Glossopteris* flora. Here again is a field in need of detailed exploration.

In conclusion, I may be permitted, as one who is approaching the terminal stages of his career, to offer a word of friendly advice to those of the younger generation of taxonomists, paleobotanists and morphologists who may become interested in the origin of the angiosperms: Look West young man toward the remnants of Gondwana Land!

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